The thermal biology of the wingless grasshopper (*Phaulacridium vittatum*). A model to test potential climate change impacts on insects

by

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The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

Rebecca M.B. Harris, June 2012

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Abstract

The study of thermal biology can contribute to our understanding of climate change by highlighting the thermal constraints affecting a species and the adaptive mechanisms available. This thesis describes the thermal biology of the wingless grasshopper (*Phaulacridium vittatum*), to highlight the characteristics that predispose some insect species to cope with, or benefit from, a changing climate. These characteristics include having a wide distribution, broad thermal tolerances, morphological plasticity and a wide range of behavioural responses to temperature.

Phaulacridium vittatum is a widely distributed cool temperate species, which exhibits plasticity in melanism and body size. Geographic variation in these characters along a latitudinal gradient was assessed, to test whether variability in body size and melanism reflect adaptations to local thermal conditions. Selection for body size was found to be mediated by different factors in males and females of the wingless grasshopper. Female body size decreased significantly with latitude, while male body size was largest at intermediate latitudes. Geographic variation in the body size of the wingless grasshopper was best explained in terms of rainfall and radiation seasonality, rather than temperature. However, the body size of males was also strongly influenced by reflectance, suggesting that thermal fitness does play a role in determining adaptive responses to local conditions in this sex.

The intra-specific application of the thermal melanism hypothesis was tested, firstly by measuring the thermal properties of the different colour morphs in the laboratory, and then by comparing the average reflectance and spectral characteristics of populations along altitudinal gradients in Tasmania. Melanism in *P. vittatum* represents a gradation in colour rather than distinct colour morphs, with reflectance ranging from 2.49 to 5.65%. In unstriped grasshoppers, darker morphs warmed more rapidly than lighter morphs and reached a higher maximum temperature (lower temperature excess). No significant differences in thermal quality were found between the colour morphs of striped grasshoppers. In support of the thermal melanism hypothesis, grasshoppers were, on average, darker at higher altitudes; there were differences in the spectral properties of brightness and chroma between high and low altitudes; and temperature variables were significant influences on the average reflectance of

female grasshoppers. However, the relationship between melanism and altitude was not consistent across all gradients, demonstrating the importance of habitat differences, and the benefit of studying trends across replicated gradients.

The range of thermal conditions typically available to ground-dwelling insects in a cool temperate region was quantified using field measurements of microhabitat temperatures over the period of a year. A steady state biophysical model was developed to predict the operative temperature of a grasshopper, in the absence of behaviour, under varying conditions of temperature, radiation, and wind. The heat capacity of the grasshopper was determined in a passive warming experiment, and used to develop a transient model that enabled thermoregulatory behaviour to be considered. These results were related to the preferred temperature of *P. vittatum* measured in thermal gradients in the laboratory, illustrating the extent to which microhabitat variability can provide a range of thermal opportunities and potentially alleviate the impacts of climate change on a small ectotherm.

The importance of melanism in insect thermoregulation was tested using theoretical and experimental approaches. The biophysical model was used to identify the extent to which melanism contributes to the heat balance of small ectotherms across a range of body sizes and reflectance. In the absence of behaviour, the limiting factor in the heat balance was found to be the degree of melanism, rather than small body size alone. However, in the absence of extreme melanic forms, when behaviour is incorporated by accounting for movement between sun and shade, slight differences in warming times may accumulate to amplify any thermal difference due to melanism.

To test whether preferred temperature is a plastic response to ambient temperature, and whether melanism affects behaviour, the preferred temperature of the colour morphs of *P. vittatum* was determined in a laboratory thermal gradient, before and after manipulating body colour by painting. The preferred temperature of the darkest colour form was significantly higher than that of the lightest form (with a mode of 37.5 – 40.0°C, compared to 22.5 – 25.0°C). Painting led to changes in preferred temperature, demonstrating that thermoregulatory behaviour through habitat selection is a plastic response to changes in the

thermal balance driven by melanism. The laboratory results were supported by measurements of live populations in natural situations.

Behavioural experiments were used to determine the means by which *P. vittatum* regulates its body temperature in natural situations and under artificial warming conditions in laboratory experiments. Common thermoregulatory behaviours were found to be timing of activity, choice of substrates with optimum surface temperatures, and specific behavioural postures such as stilting and vertical orientation. Behavioural responses were constant and covered a range of spatial scales, from several centimetres to many metres, and temporal scales from seconds to hours. Measurements of preferred temperature, upper critical temperature threshold (CT_{max}) and the Maximum Voluntarily Tolerated temperature (MVT) indicated that *P.vittatum* has a broad thermal tolerance, which is further extended by the existence of the different colour morphs.

The flexible thermal biology of *P. vittatum* suggests that it has the potential to cope with climate change without the need for significant adaptation or shifts in distribution. This has consequences for its status as an important agricultural pest in Australia, and highlights the potential for other generalist herbivores with similar characteristics to respond to changing climatic conditions.

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Chapter 1 : General Introduction

The impacts of climate change on organisms are frequently divided into effects on physiology, phenology and distribution (Hughes 2000), and there are now many examples of species responding in one or more of these ways (Root *et al.* 2003, Parmesan 2006, Parry *et al.* 2007). However, the need for better understanding of the mechanisms behind species-level responses to climate change has been emphasised in several recent reviews (Hughes 2003, Hennessy *et al.* 2007). The lack of data on geographic distribution and ecological responses has been highlighted as a serious impediment to our ability to predict, adapt to or mitigate the impacts of climate change.

Many recent attempts to predict species responses to climate change have used bioclimatic models based on species distribution records. These correlative habitat models describe the relationship between the distribution of a species across the landscape with physical or biotic factors (Kearney 2006), and have been useful in identifying priority areas for conservation (Araújo *et al.* 2004), and assessing potential range shifts (Berry *et al.* 2002, Araújo *et al.* 2005), extinctions (Thomas *et al.* 2004) and invasions (Herborg *et al.* 2007, Mika *et al.* 2008).

However, improvements in the prediction of species responses can be achieved by considering the dynamic interaction of a species with its environment, using a more mechanistic approach (Kearney 2006). This enables changing influences and interactions to be considered, rather than assuming that the determinants of current distributions will remain static into novel situations, such as those expected to occur under a changing climate (Kearney 2006). Implicit in this approach is the importance of studying the interaction between a species and environmental and climatic factors at scales relevant to the animal.

The interaction between an animal and its environment is to a large extent determined by its thermal biology. This can be characterised by the availability of thermal opportunities within a habitat, thermoregulatory behaviour, and physiological and

morphological characteristics such as colour and body size (Christian & Weaver, 1996). These factors will determine the ability of a species to cope with the changes that are expected to occur under a changing climate.

The most recently published climate change projections for Australia suggest that within 800km of the coast, annual mean temperatures will be 0.1 to 1.3°C higher by the year 2020 (relative to 1990), potentially rising to 0.4 to 6.7°C by 2080 (Hennessy et al. 2007). Associated with elevated temperatures will be increases in potential evaporation and heatwaves, fewer frosts and an increase in variability (Hennessy et al. 2007). Annual mean rainfall is predicted to decrease across Australia, but, as with temperature, patterns differ across seasons and regions (Hughes 2003, Hope & Foster 2004, Suppiah *et al.* 2004, Hennessy *et al.* 2007).

The study of thermal biology can contribute to our understanding of climate change by highlighting the thermal constraints affecting a species and the adaptive mechanisms available (Helmuth *et al.* 2005). Animals can respond in several ways to changes in their thermal environment. The most immediate way is behavioural or physiological change, which is rapid and reversible (Angilleta *et al.* 2002). However, behavioural thermoregulation may not be entirely effective in buffering thermal extremes, or may become too costly in terms of time and energy expended (Huey & Slatkin 1976). Adaptive shifts in temperature tolerance then become necessary, either through phenotypic plasticity in the short term or through longer term genetic adaptation (Christian *et al.* 1983, Angilleta *et al.* 2002, Gienapp *et al.* 2008). The potential for adaptation to climate change will be limited by the extent to which geographic variation is due to genetic differences between populations and how much is due to phenotypic plasticity of individuals growing in different environments. Where morphology and physiology is narrowly constrained by genotype, adaptability will be limited in the short term. In contrast, species that exhibit phenotypic plasticity have greater adaptive potential in the short to medium term.

1.1 Aims and Objectives

The primary aim of this thesis is to describe the thermal biology of the wingless grasshopper (*Phaulacridium vittatum*) and its importance in the context of climate change.

Phaulacridium vittatum is a major agricultural pest in Australia, causing extensive damage to grazing pasture and high value crops such as grapes, vegetables, fruit and tree nurseries (Milner 2001). An understanding of its thermal biology will contribute to its management under changing climatic conditions. However, while I focus on one species, I aim to generate information relevant to other small ectotherms, and to illustrate the potential impact of climate change on insects, which make up the bulk of biodiversity and are responsible for much of the functioning of all ecosystems (Wilson 1987).

The wingless grasshopper is an appropriate model species because it is a common, widely distributed species that exhibits variability in melanism and body size, and actively regulates its body temperature through behavioural means. Grasshoppers are one of the most abundant groups of ectotherms that are active behavioural thermoregulators (Uvarov, 1966; Willott, 1997; Klass, 2004), and are found in a diverse range of habitats around the world (Chappell 1983, Chappell & Whitman 1990).

To incorporate the factors described above that influence the adaptability of a species to changing conditions, I have combined a broad geographical approach with biophysical and behavioural ecology, to link the morphological and behavioural aspects of thermal biology with microclimatic variability.

In order to achieve the primary aim, this thesis addresses the questions:
1. Are the biophysical properties body size and melanism important in determining the interaction between *P.vittatum* and its environment?

2. Does variability in body size and melanism reflect adaptation to local conditions?
3. What thermal conditions is a ground-dwelling insect exposed to within a cool temperate region?
4. What are the thermal requirements of *P.vittatum*? Does morphological and physiological plasticity increase thermal flexibility?
5. To what extent can *P.vittatum* regulate its body temperature through behavioural means?
6. What is the interaction between morphology, physiology and behaviour in thermoregulation?

In Chapter 2, geographic variation in body size and melanism along a latitudinal gradient is assessed, to determine the range in variability of body size and melanism that exists in *Phaulacridium vittatum.* These characteristics play an important role in determining the interaction of a species with its thermal environment, and broad-scale geographic patterns can be assessed to test whether variability in these characters reflect adaptations to local thermal conditions. This chapter has been published in *The Journal of Biogeography* as Harris, R.M.; McQuillan, P. and Hughes, L. (2012) "Patterns in body size and melanism along a latitudinal cline in the wingless grasshopper, *Phaulacridium vittatum*".

In Chapter 3 altitudinal gradients in body size and melanism are investigated, to test the intra-specific application of the thermal melanism hypothesis. The thermal properties of the different colour morphs found in *P. vittatum* are quantified and the spectral characteristics of populations along altitudinal gradients in Tasmania are compared. The underlying causes of clines in melanism are considered, by assessing correlations between reflectance, body size and climatic variables. This chapter has been submitted to the *Journal of Insect Science*, as Harris, R.M.; McQuillan, P. and Hughes, L. (20xx) "A test of the thermal melanism hypothesis in the wingless grasshopper (*Phaulacridium vittatum*)".

The importance of scale when considering the potential impacts of climate change on insects is addressed in Chapter 4. The aim of this chapter is to quantify the range of thermal conditions typically available to ground-dwelling insects in a cool temperate region, and to predict the operative temperature of a grasshopper under varying conditions of temperature, radiation, and wind. The extent to which microhabitat variability can provide a range of thermal opportunities and potentially alleviate the impacts of climate change on a small ectotherm is illustrated. This chapter has been submitted to PLoS ONE as Harris, R.M.; Nunez, M.; Hughes, L. and McQuillan, P. (20xx) "Insects do not live in a mean world – can microhabitat variability alleviate climate change impacts on insects?".

In Chapter 5 the relative importance of body size and melanism in insect thermoregulation is tested using theoretical and experimental approaches. A biophysical model is developed to identify the extent to which melanism contributes to the heat balance in the absence of behaviour across a range of body sizes and reflectance. To test whether preferred temperature is a plastic response to ambient temperature, and whether melanism affects behaviour, the preferred temperature of the colour morphs of *P. vittatum* is determined in a laboratory thermal gradient, before and after manipulating body colour by painting. Live body temperatures of the colour morphs in natural situations is also compared. This chapter will be submitted to *Oecologia*, as Harris, R.M.; McQuillan, P. and Hughes, L. (20xx) "When is small too small? The importance of melanism in insect thermoregulation".

Thermoregulatory behaviour can reduce exposure to high and variable temperatures, enabling body temperatures to be maintained within preferred ranges. The extent to which behaviour is able to increase the thermal flexibility of a species is covered in Chapter 6. The main thermoregulatory behaviours used by *P. vittatum* in natural situations and under artificial warming experiments are described. The thermal tolerance of *P. vittatum* is determined by measuring the preferred temperature, upper critical temperature threshold (Ct_{max}) and the Maximum Voluntarily Tolerated temperature (MVT). The range of colour morphs is tested to investigate the interaction between behavioural and morphological plasticity. Chapter 6 is intended

for submission to *The Journal of Insect Science* as Harris, R.M.; McQuillan, P. and Hughes, L. (20xx). “The importance of behavioural thermoregulation in the wingless grasshopper (*Phaulacridium vittatum*).”

Chapter 7 presents a synthesis of all the results and a general discussion of the implications of the thermal biology of *P.vittatum* for its pest status under a changing climate.

Chapters are in the form of papers to be submitted for publication in scientific journals. They are intended as stand-alone papers that address research questions or current issues that were identified during the development of the thesis. As a result, there is some repetition between the chapters, and in some cases data may be presented more than once, or analysed in different ways. Detailed literature reviews and justification of the approaches taken are provided in the introduction of each chapter.

1.2 References

Angilleta MJ, Niewiarowski PH, Navas CA (2002) The evolution of thermal physiology of ectotherms. *Journal of Thermal Biology*, **27**, 249-268.

Araújo MB, Cabezas M, Thuiller W, Hannah L, Williams PH (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, **10**, 1618-1626.

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1504-1513.

Berry PM, Dawson TP, Harrison PA, Pearson RG (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, **11**, 453-462.

Chappell MA (1983) Metabolism and thermoregulation in desert and montane grasshoppers. *Oecologia*, **56**, 126-131.

Chappell MA, Whitman DW (1990) Grasshopper Thermoregulation. In: *Biology of Grasshoppers* (eds Chapman RF, Joern A), pp. 43-172. Wiley and Sons.

Christian K, Tracy CR, Porter WP (1983) Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology*, **64**, 463-468.

Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783-786.

Gienapp P, Teplitsky C, Alho JS, Mills JA, Merila J (2008) Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology*, **17**, 167-178.

Helmuth B, Kingsolver JG, Carrington E (2005) Biophysics, physiological ecology and climate change: does mechanism matter? *Annual Review of Physiology*, **67**, 177-201.

Hennessy K, Fitzharris B, Bates BC, *et al.* (2007) In: *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*(ed Parry ML, O.F. Canziani,J.P. Palutikof, P.J. van der Linden and C.E. Hanson), pp. 507-540. Cambridge University Press, Cambridge, UK.

Herborg L-M, Jerde CL, Lodge DM, Ruiz GM, MacIsaac HJ (2007) Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecological Applications*, **17**, 663-674.

Hope P, Foster I (2004). Indian Ocean Climate Initiative.

Huey RB, Slatkin M (1976) Cost and Benefits of Lizard Thermoregulation. *The Quarterly Review of Biology*, **51**, 363-384.

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution*, **15**, 56-61.

Hughes L (2003) Climate change and Australia: Trends, projections and impacts *Austral Ecology*, **28**, 423–443.

Jeschke JM, Strayer DL (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Science*, **1134**, 1–24.

Kearney M (2006) Habitat, environment and niche: what are we modelling? *Oikos*, **115**, 186-191.

Mika AM, Weiss RM, Olfert O, Hallett RH, Newman JA (2008) Will climate change be beneficial or detrimental to the invasive swede midge in North America? Contrasting predictions using climate projections from different general circulation models. *Global Change Biology*, **14**, 1721-1733.

Milner R (2001) In: *Association of Applied Acridology International Biocontrol working group newsletter 1*(eds Hunter D, Lomer C).

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637-669.

Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? *Global Ecol Biogeography*, **12**, 361-371.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57-60.

Suppiah R, Whetton PH, Watterson IG (2004).

Thomas CD, Cameron A, Green RE, *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145-148.

Wilson EO (1987) The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology*, **1**, 344-346.

Chapter 2: Patterns in body size and melanism along a latitudinal cline in the wingless grasshopper (*Phaulacridium vittatum*).

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Chapter 3: A test of the thermal melanism hypothesis along in the wingless grasshopper (*Phaulacridium vittatum)*

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Chapter 7: General Discussion. The thermal biology of the wingless grasshopper (*Phaulacridium vittatum*), and implications for its pest status under a changing climate.

7.1 Introduction

There is now extensive evidence documenting substantial and widespread impacts of climate change on plants and animals around the world, including changes to species distributions, abundance, phenology and community composition (reviewed by Walther *et al.* 2002; Hughes 2003; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2007). However, not all species will be negatively affected. By studying the thermal biology of *Phaulacridium vittatum,* I have highlighted many of the characteristics that predispose a species to cope with, or benefit from, a changing climate. These include having large population sizes and wide ranges, resulting from broad thermal tolerances, phenotypic plasticity in morphology, and a wide range of behavioural and physiological responses to temperature (Williams *et al.* 2008; Chown *et al.* 2010).

While many of the methods I have used are well established in the thermal biology literature, it is unusual for so many aspects to be collected for one species. Further, their application to questions relevant to climate change has not been widely made. For example, by describing insect behaviour in the laboratory and in natural situations, I have highlighted the potential for the interaction between morphological and behavioural plasticity to greatly enhance the ability of a species to cope with changing conditions. By integrating empirical, species - level information with fine scale measurements of microclimate I have successfully described potential responses to climate change at a scale relevant to biological processes. Using biophysical models of heat exchange I have applied information gained from one species to consider other small ectotherms in a theoretical context.

The aim of this chapter is to synthesise the results of the previous chapters within the context of existing knowledge of *P.vittatum,* and consider the implications for its pest status under a changing climate. Although I have focused on one species of insect, the results are illustrative of the potential capacity for other small ectotherms with similar

characteristics to cope with temperature change. Conversely, many species do not possess these characteristics, and these species are likely to more susceptible to change.

7.2 The thermal biology of *P.vittatum*

Throughout this thesis I have demonstrated that *P.vittatum* has many of the characteristics of a species likely to benefit from the more variable, elevated temperatures and decreased rainfall that are projected to occur in many regions under climate change. These include phenotypic plasticity in morphology, physiology and behaviour.

7.2.1. Morphological plasticity

Over the extent of its latitudinal range, *P. vittatum* exhibits variability in body size and colour (Chapter 2), two characteristics that influence the interaction of a species with its thermal environment (Chapter 5) and provide opportunities for adapting to changing conditions. Femur length, a surrogate for body size, ranged from 9.08-12.00mm in wingless females and from 6.98 - 9.62mm in wingless males. Male weight ranged from 0.029 - 0.196g and female weight ranged from 0.067 - 0.332g. Winged grasshoppers fell within these ranges (femur length 7.2-11.5mm; weight 0.094-0.228g). Average reflectance ranged from 2.17 - 4.96% across the latitudinal range of the species and 2.49 - 5.65% across altitudinal gradients within Tasmania.

Geographic variability in body size and melanism was driven by different factors in male and female grasshoppers (Chapter 2). Female body size decreased with latitude, while males were largest at intermediate latitudes. Variability in body size was influenced by climatic conditions, in particular radiation seasonality (females only) and annual rainfall (males and females). Female body size was more responsive to changes in local conditions than reflectance, and was unrelated to reflectance. The opposite was true for male grasshoppers, in which variability in body size appeared to be compensated for by changes in melanism, with darker males generally being smaller than lighter males. Female body size may be less related to thermal conditions than to climate variables that would determine food availability and quality, with consequences for fecundity, while male body size reflects thermoregulatory fitness.

The existence of altitudinal clines in average reflectance, with darker grasshoppers predominant at higher altitudes, supports the hypothesis that melanism develops in

response to local thermal conditions (Chapter 3). At the regional scale of the altitudinal study, reflectance was correlated with temperature (females) and rainfall (males), but there was no correlation between reflectance and body size in either sex. The different patterns demonstrated between the latitudinal and altitudinal studies suggest that the wingless grasshopper is able to respond to local conditions either through changes to reflectance or body size, or both, depending on site-specific conditions such as the openness of the habitat.

Variability in colour provides greater thermal flexibility for this species (Chapters 3, 5 and 6). *Phaulacridium vittatum* is polymorphic for colour and pattern, with individuals ranging from light through to dark brown and black, and rarely, green. They can be striped, unstriped, or patterned. The thermal characteristics of the colour morphs were found to be significantly different (Chapter 3), and relatively small differences in colour were sufficient to change the time taken to reach upper thermal limits under high radiation levels (Chapter 4). The cumulative effect of such differences over the course of the day, particularly in heterogeneous environments where shuttling between sun and shade is frequent, would be sufficient to have consequences for fitness under changing climatic conditions.

In addition to the purely biophysical effects of melanism, the existence of different colour morphs serves to extend the range of temperatures tolerated by *P.vittatum*. Live body temperatures measured for the darkest unstriped morph in natural situations was 2°C higher than those of the lightest morphs (28.8°C compared with 26.3°C), and the preferred temperature and the upper critical temperature threshold (Ct_{max}) were also significantly higher (Chapters 5 and 6). These results highlight the potential for the interaction between morphological and behavioural plasticity to greatly enhance the ability of a species to cope with changing conditions.

7.2.2. Behavioural flexibility

Although the wingless grasshopper is best adapted to cool temperate conditions, it is commonly found in habitats where it is regularly exposed to very high surface temperatures (Chapter 4). For example, in exposed pasture at low altitude in Tasmania, average daily maxima exceeded 40°C in sunny conditions, and even at high altitudes surface temperatures above 35°C were commonly measured. The biophysical model I

developed for *P.vittatum* predicted operative body temperatures of more than 50°C under conditions such as these, in the absence of behavioural thermoregulation. However, I have demonstrated in several ways that *P.vittatum* uses behavioural means of thermoregulation to take advantage of the range of thermal opportunities available within heterogeneous habitats. It has adapted to cope with high and variable temperatures and is a good example of a species that could be expected to cope with a considerable degree of climate change without the need to change its distribution.

Live body temperatures measured across the full extent of the eastern distribution of *P.vittatum* were generally maintained within the range of 25-30°C, regardless of local surface temperatures. The exception to this was data collected from specimens at two forested sites, representing marginal habitat, at which live body temperatures were significantly lower than other populations (Chapters 5 and 6).

I have demonstrated that *P.vittatum* is able to maintain body temperatures within the preferred temperature range by means of substrate choice, timing of activity and postural adjustments (Chapter 6). Behavioural responses take place at a range of spatial scales, from several centimetres to many metres, and temporal scales, from seconds to hours. At the study sites, available temperatures ranged up to 35°C between open and more sheltered microhabitats, and temperatures were highly variable, even at the scale of centimetres (Chapters 4 and 6). At the site scale, grasshoppers select microhabitats on the basis of their thermal quality, which changes over the course of the day. Vertical orientation, stilting and shade seeking were shown to be highly effective at keeping body temperatures tolerable in the face of increasing temperature.

The transient model also demonstrated that changes to body temperature are rapid for small insects such as *P.vittatum*, particularly when shuttling between sun and shade, when preferred temperatures can be achieved within seconds (Chapter 4). As long as some shade is available, grasshoppers will be able to maintain body temperatures within the preferred range, even with large increases in ambient temperature. Because *P.vittatum* is a generalist herbivore, the fitness costs of thermoregulation are not likely to be high. Adults are able to eat a range of plant species, so moving up vegetation or into shaded areas will not incur costs such as lost foraging and mating opportunities. Since the size and scale of

movement of the grasshopper is so small, the heterogeneity required to provide sufficient thermal opportunities is not great, and its status as an important agricultural pest is unlikely to be challenged by rising temperatures under climate change.

Preferred temperature was found to be a plastic behavioural trait, responding to ambient temperature, rather than being genetically determined (Chapter 5). When colour was manipulated experimentally in live grasshoppers, preferred temperature changed to reflect the thermal qualities of the new colour. The preferred temperature of light grasshoppers increased after they were painted black, and decreased after being painted white. Similarly, dark individuals that were painted white behaved like a light individual, maintaining a lower body temperature. This is strong evidence to support the ability of *P.vittatum* to cope with variable and increasing temperatures.

It has been suggested that while behavioural thermoregulation will provide a short-term buffer against the impacts of climate change, in the long-term it may inhibit adaptation to climate change since it reduces exposure to elevated temperatures (Huey, Hertz & Sinervo 2003). Effective thermoregulation may reduce the intensity of selection on other traits necessary to adapt to climate change in the long term. However, the wingless grasshopper not only uses behavioural methods to adjust to variable temperatures, it has a broad temperature tolerance and variability in morphology and physiology. It will likely be at an advantage as the costs associated with thermoregulation increase and adaptive shifts in temperature tolerance become necessary (Angilleta, Niewiarowski & Navas 2002).

7.2.3. Broad thermal tolerance

Thermal tolerance traits are important determinants of the likelihood that a species will become invasive, spread into new areas or reach outbreak population levels within current distributions (Slabber *et al.* 2007; Ward & Masters 2007). *Phaulacridium vittatum* has a broad thermal tolerance, suggesting a high degree of physiological plasticity (Chapter 6). The range in preferred temperature is high within populations and even within individuals (Chapter 5). As discussed above, the existence of different colour morphs extended the range in preferred temperature of the species. The darkest unstriped morph exhibited a mean preferred temperature of 34.4 ± 2.1°C in the laboratory, compared to live body

temperatures of 28.8 ± 0.18°C, suggesting that it can tolerate high temperatures when necessary.

Additionally, *P.vittatum* may be able to mount a behavioural fever in response to fungal infection (Ouedraogo, Goettel & Brodeur 2004). Although I did not test for the presence of fungi, the bimodal distribution of preferred temperature found in the laboratory, with a high peak in the region of 35-40°C, was not exhibited in natural situations. Further research would be worthwhile because of the implications this flexibility in thermal tolerance has for species interactions under future climate change (discussed below).

It has been suggested that insects are inherently less able to adapt to changes at the higher limits to their temperature tolerance than at the lower limits (Gaston *et al.* 2009). Lower thermal limits show greater variation and a more plastic response to acclimation than do upper critical limits (Lutterschmidt & Hutchison 1997; Gaston & Chown 1999; Terblanche *et al.* 2005). However, the high values for the maximum voluntarily tolerated temperature (MVT) and critical thermal maxima (CT_{max}) (Chapter 6) found for *P.vittatum* suggest that it has the potential to cope with increasing temperatures without the need for significant adaptation.

7.3 Implications for pest status

As I have demonstrated for *P.vittatum*, not all species will be negatively affected by climate change, and one area of concern is the potential positive impact of changing conditions on pest species. Possible consequences include the spread of pest species into new areas, changes to inter-specific interactions and increases in the scale and frequency of outbreaks, caused by changes in population growth rates or increases in the number of generations per year (Porter, Parry & Carter 1991; Ward & Masters 2007).

7.3.1. Changes to current distribution

Phaulacridium vittatum is currently distributed in south-eastern Australia, Tasmania and south-western Australia, with a latitudinal range of -23° 36’ to -43° 06’S, and an altitudinal range from sea-level to 1500m. Based on my collections and records held at the Australian National Insect Collection, CSIRO, Canberra, I mapped the current distribution of the wingless grasshopper (Figure 7.1) using MaxEnt Version 3.2.0

(Phillips, Anderson & Schapire 2006). The potential distribution is based on 19 bioclimatic variables generated by WorldClim (Hijmans *et al.* 2005).

The variables with the greatest contribution to the current distribution model were temperature seasonality (BIO4 - 26.2%), rainfall of the coldest quarter (BIO19 -20.8%), isothermality (BIO3 - 20.1%) and mean temperature of the coldest quarter (BIO11 15.8%). The jackknife test of variable importance showed that the highest gain in isolation was from isothermality (BIO3), followed by temperature seasonality (BIO4) and the mean temperature of the coldest quarter (BIO11).

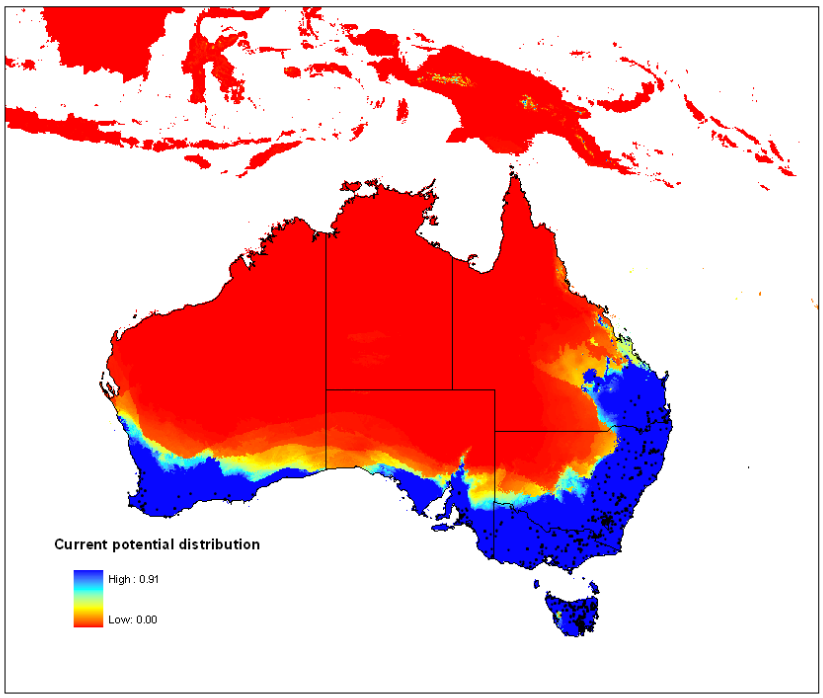

Figure 7-1: Current potential distribution of *P.vittatum*. Dots show collection localities (n = 1625).

The wide range currently shown by *P.vittatum* is unusual for a relatively small species of grasshopper in Australia. This is most likely due to its broad temperature tolerance, and the large population sizes and dispersal ability exhibited under optimal conditions. Although the dispersal abilities of wingless individuals are limited, winged grasshoppers can disperse over substantial distances in a series of short flights. The genetic potential for wing growth is realised under conditions of high temperature and population density,

and under these conditions dispersal can be significant (Baker 2005). Population sizes of *P. vittatum* are commonly very large in optimum habitats such as dry, overgrazed pasture, and dense populations of 50-100 m^{-2} may occur during outbreaks (Baker 2005).
On a broad scale the current distribution of the wingless grasshopper is determined primarily by temperature and rainfall, with dryness limiting its distribution towards inland Australia. As these variables change over the next century, shifts in the favourability of some regions for *P.vittatum* will follow. Figure 7.2 shows the projected distribution of *P.vittatum* in 2050 and 2080 generated in MaxEnt Version 3.2.0 (Phillips, Anderson & Schapire 2006), based on climate change projections obtained using the Delta statistical downscaling method in WorldClim (Hijmans *et al.* 2011). The CSIRO Mk3 model was used because it applies a greater number of latitude and longitude points over Australia and is widely used in similar studies in Australia. The SRES A2 emissions scenario was used to illustrate changes that are reasonably likely to occur under conditions of high population growth and slower adoption of technological advances (IPCC 2007). This scenario projects a temperature change of between 2.0-5.4°C relative to 1980-1999.

Changes to the distribution are projected to occur primarily at the northern limit in south-eastern Queensland and in inland regions currently limited by low rainfall such as south-western NSW. By 2050, these areas are less favourable for *P.vittatum.* In contrast, the distribution in south-western Australia and some regions in central Queensland expand under the projections to 2050. By 2080, some of these shifts are reversed. For example, the potential distribution in the south-west of Australia has contracted compared to the current limits, while the NSW distribution expands again to exceed that under current climatic conditions.

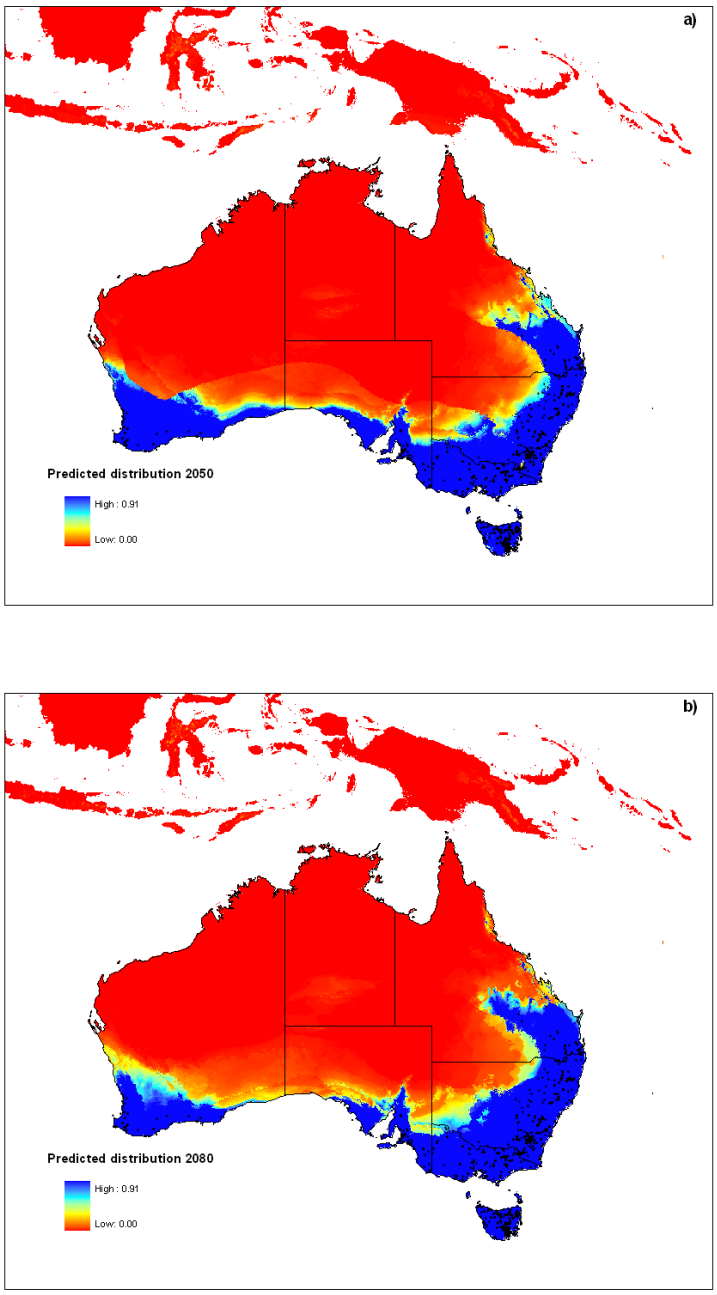

Figure 7-2: Predicted distribution of *P.vittatum* in a) 2050 and b) 2080. Dots show collection localities (n = 1625).

With increased cloud cover, which is projected for some regions (IPCC 2007), the ability of the wingless grasshopper to maintain preferred body temperatures under elevated temperatures would be greatly enhanced. However, at low ambient temperatures, such as at high altitudes where activity times are restricted due to low temperatures, increased

cloud cover may lead to the lower temperature threshold becoming limiting, rather than the upper threshold, because of the importance of solar radiation in thermoregulation.

While the potential range of *P.vittatum* is driven by broad-scale climatic factors, the extent to which its distribution will shift in response to broad scale climatic change will be strongly affected by topography, an important determinant of local climate and moisture regimes. It will be further mediated by microhabitat heterogeneity, as demonstrated in Chapter 4, and by ecological factors such as the availability of food plants and suitable substrate for egg laying, which are largely influenced by soil type and seasonality of rainfall. The limiting role of food availability is demonstrated by the spread of *P.vittatum* in recent years to dry regions that were previously unsuitable. This spread has been mediated by the introduction of drought-tolerant pasture species such as Lucerne (*Medicago sativa*) and the spread of weeds such as Paterson's Curse (*Echium plantagineum*), which are good food sources (Oliver & Croft 2010).

Ultimately, the ability of a species to persist in an area under changing conditions or spread into a new area will be determined by the thermal requirements of the least mobile life stage (Kingsolver *et al.* 2011). Damage by pests will still be extensive in cases where mobile adults with high behavioural flexibility are able to disperse into new areas, but establishment will be limited. In the case of *P. vittatum*, where the least mobile life stage is the egg stage, increases in ambient temperature will be alleviated by the damping effect of being buried in soil. In many cases, immobile life stages have a higher temperature tolerance, which then declines in subsequent stages (Bowler & Terblanche 2008). For example, the preferred temperature of the desert locust (*Schistocera gregaria*) becomes progressively higher between the first and fifth instar nymphs (from 29.4°C to 36.7°C) (Bodemheimer (1929) cited by Deal 1941). Further study into this aspect of the thermal biology of *P. vittatum* would improve projections on its rate of spread and future distribution.

7.3.2. Outbreaks

Outbreaks of *P. vittatum* have been recorded in Australia since 1935, but have become more severe and frequent since the 1950's. This is largely due to the expansion of improved pasture, while acid soils exacerbate the problem by encouraging favoured food

plants such as broad-leaved weeds (Baker 2005), and overgrazing provides ideal egg laying opportunities by opening up the inter-tussock space (Roberts 1972).

Currently, outbreaks of *P. vittatum* occur in dry summers following years in which high summer/autumn rainfall has fallen. Dry conditions reduce the populations of natural parasites such as sceleonid wasps, mermithid nematodes and fungi, and summer rain encourages the growth of green feed for nymphs. Reductions in annual rainfall are projected to occur over much of Australia, but summer rainfall has increased in some regions in the east and north of Australia (Hennessy *et al.* 2007). Even in regions where summer rainfall is expected to decline, such as south-western Western Australia, the spread of food plants has reduced the dependency of *P. vittatum* on high seasonal rainfall. The frequency and severity of outbreaks of *P.vittatum* is therefore likely to increase in large parts of its range under climate change.

7.3.3. Changes to species interactions

The presence of parasitic fungi, wasps and nematode worms are important determinants of the local distribution of *P.vittatum* (Fargues *et al.* 1997), which is generally found in areas where densities of these parasites are lowest, such as on drier ridges and away from tree-lines. The spread of improved pasture has not only improved food availability for *P. vittatum,* but has also reduced the distribution of the natural parasites of *P. vittatum* through destruction of their habitat. The natural parasites are also less mobile and less effective thermoregulators than *P. vittatum*. For example, the fungus *Beauveria bassiana*, which is a significant natural mortality factor for *P. vittatum*, has a well- defined thermal threshold of 35-37°C (Fargues *et al.* 1997).

In the past decade, control of outbreaks of *P. vittatum* has shifted away from the spraying of chemical insecticides because of concerns over residues and the killing of non-target species that are important natural parasites of the grasshopper. Chemical control is also only effective in the short-term, with populations of wingless grasshoppers often re-invading within 1 to 2 weeks (Milner 2001). Instead, spraying with the bioinsecticide *Metarhizium anisopliase* var. *acridium* has become more common. However, this fungus is known to be sensitive to temperature extremes, being most effective at 25-30°C (Lomer 2001). Since most damage to crops occurs during the warmer months of December to March, this raises the possibility that with increases in temperature under climate change,

combined with decreases in rainfall, effective control of acridid grasshoppers may become more difficult (Blanford, Thomas & Langewald 1998; Hance *et al.* 2007).

Changes to atmospheric composition can alter aspects of the interaction between food plants and their consumers. Elevated carbon dioxide (CO_2) has been shown to reduce the uptake of nitrogen by plants, leading to a reduction in food quality for herbivores (Johns & Hughes 2002). In some insect herbivores, consumption has been shown to increase to compensate for the poorer food quality, but there may also be flow-on effects on fecundity and larval survival (Johnson & McNicol 2010). Susceptibility of host plants to herbivory may also be affected by elevated CO_2 (Martin & Johnson 2011). Research into interactions such as these would be necessary in order to predict the possible consequences for crop damage by *P. vittatum* in the future.

7.3.4. Increases in the number of generations per year

The number of generations an insect produces in a year is influenced by climatic conditions and photoperiod (Bale *et al.* 2002). Faster growth, longer growing seasons and milder winters under climate change are leading to shifts from univoltine to bivoltine life cycles in some insects (Altermatt 2010). There is anecdotal evidence that the wingless grasshopper shifts to a bivoltine life cycle under "unusual conditions" (Emery 2005), and a partial second generation has been recorded in parts of NSW (Baker 2005). If a sustained shift in voltinism were to occur, damage to crops would increase in severity and frequency. However, more than one generation per year would require alterations to the extended egg diapause that *P. vittatum* currently undergoes, as well as a continuous food supply for emerging nymphs. Further research into diapause regulation in *P. vittatum* is required to determine whether diapause length is obligate and requires a breaking cue, or facultative and responsive to environmental conditions (Scriber, Ording & Mercader 2008).

P. vittatum is to a certain extent pre-adapted to climate change, and is likely to benefit under a changing climate. It is a widely distributed generalist herbivore, with broad thermal tolerances, and a wide range of morphological, behavioural and physiological responses to temperature. These characteristics are shared by many temperate insect species, suggesting that these results may have wider applicability.

7.4 Conclusion

In this thesis I have made a valuable contribution to the literature on an important agricultural pest species in Australia. By describing the thermal biology of *Phaulacridium vittatum*, I have provided information that is essential to understanding its likely performance, spread and impact under future conditions. However, I have further extended this to develop generalities regarding the response of small ectotherms to climate change. I have demonstrated that many small ectotherms may be well adapted to cope with elevated temperatures under climate change, without the need to alter their distribution.

7.5 References

Altermatt, F. (2010) Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B-Biological Sciences,* **277,** 1281-1287.

Angilleta, M.J., Niewiarowski, P.H. & Navas, C.A. (2002) The evolution of thermal physiology of ectotherms. *Journal of Thermal Biology,* **27,** 249-268.

Baker, G. (2005) Wingless grasshopper. *Agfact AE.1 (fourth edition) 10 January 2005*.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology,* **8,** 1-16.

Blanford, S., Thomas, M.B. & Langewald, J. (1998) Behavioural fever in the Senegalese grasshopper, *Oedaleus senegalensis*, and its implications for biological control using pathogens. *Ecological Entomology,* **23,** 9-14.

Bowler, K. & Terblanche, J.S. (2008) Insect thermal tolerance: what is the role of ontogeny, ageing and senescence? *Biological Reviews,* **83,** 339-355.

Chown, S.L., Hoffmann, A.A., Kristensen, T.N., Angilletta, M.J., Stenseth, N.C. & Pertoldi, C. (2010) Adapting to climate change: a perspective from evolutionary physiology. *Climate Research,* **43,** 3-15.

Deal, J. (1941) The temperature preferendum of certain insects. *Journal of Animal Ecology,* **10,** 323-356.

Emery, R. (2005) Wingless grasshoppers and their control. Farmnote No. 62/90, Agdex 622.

Fargues, J., Goettel, M.S., Smits, N., Ouedraogo, A. & Rougier, M. (1997) Effect of temperature on vegetative growth of *Beauveria bassiana* isolates from different origins. *Mycologia*, **89,** 383-392.

Gaston, K.J. & Chown, S.L. (1999) Elevation and climatic tolerance: a test using dung beetles. *Oikos,* **86,** 584-590.

Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., Clusella-Trullas, S., Ghalambor, C.K., Konarzewski, M., Peck, L.S., Porter, W.P., Pörtner, H.O., Rezende, E.L., Schulte, P.M., Spicer, J.I., Stillman, J.H., Terblanche, J.S. & van Kleunen, M. (2009) Macrophysiology: A conceptual reunification. *The American Naturalist,* **174,** 595-612.

Hance, T., van Baaren, J., Vernon, P. & Boivin, G. (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology,* **52,** 107-126.

Hennessy, K., Fitzharris, B., Bates, B.C., Harvey, N., Howden, S.M., Hughes, L., Salinger, J. & Warrick, R. (2007) Australia and New Zealand. Climate Change 2007: Impacts, Adaptation and Vulnerability. *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change***,** 507-540.

Hijmans, R., Cameron, S., Parra, J., Jones, P. & Jarvis, A. (2011) WORLDCLIM - a set of global climate layers (climate grids). http://www.worldclim.org/.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25,** 1965-1978.

Huey, R.B., Hertz, P.E. & Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: A null model approach. *American Naturalist*, **161,** 357-366.

Hughes, L. (2003) Climate change and Australia: Trends, projections and impacts. *Austral Ecology*, **28,** 423–443.

IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. (ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M.Tignor and H.L. Miller). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Johns, C.V. & Hughes, L. (2002) Interactive effects of elevated CO2 and temperature on the leaf miner *Dialectica scalariella* Zeller (Lepidoptera: Gracillaridae) in Paterson's curse, *Echium plantagineum* (Boraginaceae). *Global Change Biology*, **8,** 142-152.

Johnson, S.N. & McNicol, J.W. (2010) Elevated CO_2 and aboveground-belowground herbivory by the clover root weevil. *Oecologia*, **162,** 209-216.

Kingsolver, J.G., Woods, H.A., Buckley, L.B., Potter, K.A., MacLean, H.J. & Higgins, J.K. (2011) Complex life cycles and the responses of insects to climate change. *Integrative and Comparative Biology*, **52,** 719–732.

Lomer, C. (2001) What is the place of biological control in acridid integrated pest management? Locust and grasshopper biocontrol newsletter No. 1. Association of Applied Acridology International Biocontrol

Lutterschmidt, W.I. & Hutchison, V.H. (1997) The critical thermal maximum: history and critique. *Canadian Journal of Zoology*, **75,** 1561-1574.

Martin, P. & Johnson, S.N. (2011) Evidence that elevated CO_2 reduces resistance to the European large raspberry aphid in some raspberry cultivars. *Journal of Applied Entomology*, **135,** 237-240.

Milner, R. (2001) *Beauveria bassiana* - studies on its potential for control of wingless grasshopper. Locust and grasshopper biocontrol newsletter No. 1. *Association of Applied Acridology International Biocontrol*.

Oliver, S. & Croft, D. (2010) Wingless Grasshopper. NSW Industry and Investment. *Primefact 631. Fifth edition April 2010*.

Ouedraogo, R.M., Goettel, M.S. & Brodeur, J. (2004) Behavioral thermoregulation in the migratory locust: a therapy to overcome fungal infection. *Oecologia,* **138,** 312-319.

Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology,* **13,** 1860-1872.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* **421,** 37 - 42.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling,* **190,** 231-259.

Porter, J.H., Parry, M.L. & Carter, T.R. (1991) The potential effects of climatic change on agricultural insect pests. *Agricultural and forest meteorology,* **57,** 221-240.

Roberts, R.J. (1972) A newly recognised form of pasture damage by *Phaulacridium vittatum* (Acrididae) on the northern tablelands of N.S.W. *Australian Journal of Entomology,* **11,** 257-258.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature,* **421,** 57-60.

Scriber, J.M., Ording, G.J. & Mercader, R.J. (2008) Introgression and parapatric speciation in a hybrid zone. *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects* (ed. K.J. Tilmon). University of California Press.

Slabber, S., Worland, M.R., Leinaas, H.P. & Chown, S.L. (2007) Acclimation effects on thermal tolerances of springtails from sub-Antarctic Marion Island: indigenous and invasive species. *Journal of Insect Physiology,* **53,** 113-125.

Terblanche, J.S., Sinclair, B.J., Klok, C.J., McFarlane, M.L. & Chown, S.L. (2005) The effects of acclimation on thermal tolerance, desiccation resistance and metabolic rate in Chirodica chalcoptera (Coleoptera : Chrysomelidae). *Journal of Insect Physiology,* **51,** 1013-1023.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature,* **416,** 389-395.

Ward, N.L. & Masters, G.J. (2007) Linking climate change and species invasion: an illustration using insect herbivores. *Global Change Biology,* **13,** 1605-1615.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. & Langham, G. (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology,* **6,** 2621-2626.